

Ecology, Behavior and Population Dynamics of the Wyoming or Rocky Mountain Moose, *Alces alces shirasi*

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(Text-figures 1 & 2)

I. ECOLOGY

WITHIN recent years the Wyoming moose, *Alces alces shirasi*, has markedly increased its numbers and range. A study of its ecology, behavior and population dynamics, besides its intrinsic interest, may have some practical application in terms of the light it throws on reasons for the subspecies' success.

The studies reported here are the results of work during the late springs, summers and early autumns of 1947, 1948, 1949, 1950 and 1952, and the winter of 1947-48. This work was supported by the New York Zoological Society and the University of Wyoming. The author is indebted to these institutions and to numerous individuals for help and information. Mr. James Simon, director of the Jackson Hole Research Station at the time of these observations, gave constant friendly interest and assistance without which the work would have been impossible.

The method used was close personal observation, aided by a pair of 10 × 40 binoculars, a 20-power scope and still and motion picture cameras. Moose were approached on foot, on horseback or in a jeep. On-the-spot notes were made of all observations except those at night. Nocturnal notes were recorded within an hour of the end of the observation period. Approximately eighteen hundred hours were spent in actual observation. In the census and distribution work, personal observation was supplemented by interviews with and questionnaires from personnel of Federal and State agencies, as well as numerous proprietors of guest ranches, who have been most helpful as a group.

MOOSE AND THEIR ENVIRONMENT

The moose is not only a solitary deer, but is the deer most dependent on water for its livelihood. Much of its summer food is aquatic vege-

tation and willow browse in the littoral zone of both streams and ponds. In addition to supplying food, ponds and lakes offer protection from insect pests. Non-feeding moose are often found partially submerged at the height of the fly and mosquito seasons. In 1950 A. D. Cannavina, at that time Assistant Chief Ranger in Glacier National Park, called my attention to the bright green color of the hair between the moose's toes. The pigment was extracted by a method suggested by L. W. Roberts (1953) and is believed to be chlorophyll. Possibly moose acquire this pigment when pond bottom algae are squeezed between their splayed toes. This might explain why moose show the coloring, while other large members of the deer family sharing their range do not. In addition to water and suitable food, moose seem to require a low average daily temperature. Thus they are found at relatively high elevations at the latitude of Wyoming, but not so high as to remove them from the proximity of small bodies of water. Merrill (1916) says "The moose swims well, but not rapidly. Like the caribou, his shoulders are well above the water when swimming. Stone relates how an Alaska bull two or three years old swam eight miles without showing evidence of exhaustion." Many of the ponds utilized by moose are beaver ponds. This is true to such an extent that in a good part of its range the moose is dependent on the beaver. Moose and beaver areas of distribution show a significant overlap. Hosley (1949) refers briefly to beaver-moose relationships, indicating a possible adverse effect of over-flooding of popular stands on moose food. We have never observed such effects in the Rocky Mountain area.

FOODS AND FEEDING

The moose food during the observation periods consisted principally of three types: willow,

algae and pond weeds. There was an abundant growth of the last two in the ponds west of the town of Moose, Wyoming, and several hundred hours of close observation were made of moose grazing these plants.

A note made on August 5: "... female entered ponds, leaving calf sampling sedge, willow and aspen. Female ate algae for one hour, keeping head under 10 to 25 seconds; ears were always above the water and erect, and twitching off flies. Then she went down on her knees and submerged completely except for her hump. She took large mouthfuls of algae, and when she came up she held her ears 'lop-eared.' She now stayed under about 30 to 45 seconds at a time." There are three points worthy of comment here: (1), the persistent feeding on algae; (2), the sampling, intermittent feeding of the calf, which was typically different from the consistent, steady feeding of the adult; and (3), the position of the ears, which was later observed whenever a moose submerged these organs and which suggested the possibility that the external ear might be used as a cover to prevent water from running into the external auditory meatus and canal. This seemed particularly likely as moose were observed to lower their ears before submerging them. This response was so constant in this stimulus situation as to resemble an anticipating reflex to submersion. Similar responses are known in other aquatic mammals. Algae seemed to be a preferred food, even in the presence of an abundant supply of a reputed favorite, the water lily. Moose were never observed to take water lily stems or leaves, although they grazed algae at the border of a large clump of them. Isolated instances of adult moose browsing on other plants such as sedges, sage brush and aspen were noted from time to time. Although many observations have been made of moose feeding on roots of the pond lily, *Nymphaea*, only one instance of moose eating other parts of these plants has been noted in five summers of observation. When moose eat the lily roots, the plants drift to shore and show no evidence of tooth marks on other parts.

The sampling proclivities of the first-year calves are further illustrated by the following note made on August 14: "... saw female and calf at east end of ponds. Cow was grazing algae, calf playing on edge of water at first, then started eating yellowed leaves and fruits of cow parsnip, *Heraclium*, then alternated with nibbles from meadow rue, *Thalictrum*, and willow, *Salix*."

In winter, moose have two obvious food sources. The first is the twigs of willow and aspen along the open river bottoms. Moose are found in their greatest aggregations in winter in such locations. It is also this winter browse which

seems to represent a limiting factor in the moose habitat. Evidence of over-browsing has been observed in many areas of the range. A second source of winter food is hay. This may be either some rancher's hay spread in a corral for cattle or stacked in a field, or the hay distributed by the State elk-feeding stations. When the snow starts to melt in late April, moose gather in numbers on the first patches of grass to show through. They kneel and graze in this position for as long as two hours at a time. Shortly after this grazing period they may be found browsing sage in the middle of the day.

Where there are several kinds of willow, moose often show a preference. In the Roaring Fork area northeast of Yellowstone Park, a short, yellow-stemmed variety, *Salix wolfii*, is almost untouched, while a tall, red-stemmed willow, *Salix geeyeriana*, growing intermixed with it, is over-browsed.

Where moose concentrate in winter, as in certain eastern areas of Yellowstone Park and the upper Wind River near Du Bois, Wyoming, very obvious over-browsing has affected the willow. This over-browse is made more evident by exclusion plots established in these areas by Federal and State authorities. The Yellowstone Park area is especially dramatic. Within the exclusion fence there is a dense growth of willow, while in the immediate neighborhood hardly a single willow is to be seen. As Hosley (1949) points out in his excellent survey of moose literature, the Rocky Mountain moose is much more dependent on willow than its eastern relatives. Willow and aspen make up the major part of its diet winter and summer. In summer it takes mainly the leaves but in winter it uses twigs of both genera up to a half-inch in diameter. Sage, *Artemisia*, forms a possibly unexpected part of the Wyoming moose's diet during late spring. Although these animals take conifer tips occasionally, mostly fir, they do so to a much lesser extent than in the east, where Aldous & Krefting (1946) found balsam to comprise approximately 15 per cent. of the diet. The absence of birch, *Betula*, from the Rocky Mountains excludes from local moose diet a plant which is a favorite in other areas.

In general, moose seem to have very definite preferences for certain food plants but nevertheless are able to exist on a remarkably wide variety of browse if they have to.

LOCOMOTION AND OTHER CHARACTERISTIC ACTIVITIES

Moose have as characteristic gaits a fast walk, a very smooth trot and a rather ungainly crashing canter. The first two are the modes of almost all movements by adults. Yearlings seem

to canter much more, even when not running with an adult. From the circumstances in which the young canter, the observer is led to consider the possibility that this may represent a form of play. Several checks on the speed of moose trotting gave an average of slightly more than 20 miles an hour.

The moose is an excellent swimmer. It crosses turbulent rivers such as the Snake and swims far out in large lakes quite frequently. So confident does it seem to be of its swimming ability that several moose drown in the Snake river each winter when they break through thin ice and are unable to climb out on the thicker shore ice.

Moose do considerable feeding underwater—that is, they gather food underwater and swallow it on emerging. Periods of submersion are quite constant and usually vary between 20 and 60 seconds, depending partly on the depth of the water and the length of time the moose has been feeding. Intervals above water are usually shorter than those below when the moose is actively feeding.

In common with other herbivores, moose frequent natural salt licks and salt blocks put out for stock. One heavily-utilized lick lies at the western end of the "Thoroughfare" just south-east of Yellowstone Park.

BEDS AND FORMS

Everywhere that moose were encountered more than once, I found several beds. These were simply depressions where the grass was matted down. In the fall one "wallow" was found similar to those described by Seton (1928). This wallow smelled of urine and feces. Several beds were under willows, and the willows showed low browsing in such places. In one instance I observed a young bull browsing while lying down for about twenty minutes at a distance of 25 paces from me.

ADAPTATION TO HUMAN STRUCTURES AND INFLUENCES

One reason for the success of moose in the Rocky Mountain area may well be their ability to adapt to human influences. In Yellowstone Park and those areas of what is now the Grand Teton Park where moose are in almost daily contact with human beings during the tourist season, the animals soon learn to continue their feeding and other activities apparently undisturbed. Such tolerance does have its limits, however. For example, in 1947 and 1948, 23 different moose were seen along a four-mile stretch of U. S. highway 287 just west of Togwotee Pass. Extensive road construction was undertaken in this area early the following year, and frequent checks showed only

three moose at this time. Where moose have less frequent contact with human beings they show more marked avoidance. Under the latter conditions their flight distance averages between 90 and 140 yards, compared with 20 to 50 yards where frequent contact has brought about adaptation.

During the winter, moose utilize two sorts of man-provided facilities and often become nuisances in the process. The first is the cleared highway. Moose get on to these and block traffic, failing to use the "moose turnoffs" plowed out by the highway department. They often trot ahead of an automobile for a mile or more and then stop and refuse to move. Attempts to get them to do so result in mutual irritation so that either the moose may charge the car or the driver may ram the moose. Close to one-tenth of one per cent. of the Jackson Hole moose population is killed on highways each winter.

Another facility used by moose in winter is stored hay. Ranchers often complain of moose taking hay from field stacks. Moose also come into feeding corrals and feed side by side with cattle. In the smaller elk-feeding stations, such as that at Black Rock, Wyoming, moose come in for the hay put out for the elk. Occasionally they even enter a hay barn. Under any of these circumstances they are in an approach-avoidance conflict situation. It is consequently at these times that most moose "attacks" on human beings are recorded.

PREDATORS

Man is the only significant predator affecting the moose. Accounts of other predation are so rare as to be memorable. In the vicinity of Glacier National Park there have been two reports of bear molesting moose in the last twenty years. The calf moose would be vulnerable to coyotes if it were not for the constant close protection afforded the calf by its mother.

PARASITES

Ectoparasites

During late July and August moose exhibit behavior which might indicate that they are being disturbed by ectoparasites. The ear-twitching, skin-shaking activity is apparently often a response to stable flies, *Stomoxys calcitrans*. Although an observer may often be annoyed by mosquitoes while within 40 feet of a moose, the latter rarely seems to respond to these pests. In the late winter and early spring moose are often heavily infected with the "winter tick" *Derma-centor albipectus*. If other weakening conditions are present, these ticks may be a contributing cause of "winter kills."

Endoparasites

Since the author was aware of no studies on the endoparasites of the Shiras moose, he undertook an examination of the viscera of two moose killed by hunters in September, 1947. A heavy infestation in the upper small intestine of both specimens with *Nematodirella longispiculata longispiculata* was found. A few individuals of *Trichiuris* (probably closely related to *Trichiuris ovis*) were present in the viscera of one animal. Identification was made by R. Honess of the Wyoming Game and Fish Department. Shiras moose do not aggregate to any extent and the danger of transmission of internal parasites in food and drink is therefore apparently small.

LIFE HISTORY

Breeding and Gestation

Mating of moose in Wyoming takes place from mid-September through early November. The young are born in late April and May after a gestation period of approximately 240 days. This is similar to the duration of gestation quoted from Lydekker by Asdell (1946) for the European moose. Asdell further quotes Lydekker and, for the Alaskan moose, Cahalane, to the effect that two calves is the usual number at birth. With regard to this, Merrill (1916) says (p. 83), "A cow moose usually has one or two calves at a time—very rarely three." Adolph Murie (1934) states that, "From my observations, it seems that cows have, as a rule, but one calf each. Forty-four cows were seen, in 1929, followed by one calf each, and only one cow with twins. Schierbeck states that only twenty-one, or eight per cent. of the 252 pregnant cows carried twins." Hosley (1949) suggests that the ratio of twin to single births may vary with range condition. Our observations would tend to confirm this. In the Jackson Hole area in 1948, 4 cows were observed to be accompanied by twin calves and 22 by single calves, or about 27 per cent. twin births. These data, it should be noted, were selected to preclude the possibility of duplicate counts. Reproductive success of the moose is indicated by the percentage of all cows that

were accompanied by at least one calf. A. Murie (*op. cit.*) found approximately 50 per cent. of all cows to bear a calf each year. In 1948 we observed 26 cows with calf and 21 dry ones. Range and browse were good in Jackson Hole that year.

In 1948 we were able to follow the development of an orphaned calf moose from the time she was two weeks old until she died at the age of seven months. For the first 12 weeks it was possible to weigh, measure and photograph the calf. This moose calf came in for feeding of condensed milk and water which she received at four-hour intervals throughout the 24 for the first three weeks, and then drank in increasing amounts at less frequent intervals. At five weeks of age she was consuming two quarts at each of three daily feedings. At one month she began browsing willow. During this period she was completely unrestrained except for the time of her weekly weighing and measuring.

Because of the constant close protection afforded her calf by the cow, the weights and measurements in Table 1 are practically unique. Only six items are recorded under chest girth, for two reasons. The calf was measured while she was drinking her milk and she often finished the bottle before this last measurement in the series could be made; also, she grew more restless while the tape was passed around her chest than during any other measurement. These data are in agreement with those of Kellum as quoted by Hosley (1949), but are somewhat lower than some earlier estimates. The increase in face length between the seventh and ninth week marks a turning point in heterogonic growth from the typical short-faced calf to the more adult type. This sudden change has been confirmed by field observation and should be useful for the experienced observer in determining whether a calf is more or less than two months of age. At three months the calf's coat color starts to change from a fuscous red-brown to the typical adult agouti color.

Suckling is very difficult to observe, since it usually takes place in secluded locations. The

TABLE 1. GROWTH OF A MOOSE CALF. (ALL LINEAR MEASUREMENT IN MILLIMETERS)

Weeks of age	2	3	4	5	6	7	9	11	13
Shoulder height	813	838	864	876	876	940	1092	1118	1143
Total length	914	991	1067	1092	1181	1181	1346	1448	1626
Occiput-muzzle	279	279	305	305	305	305	368	381	381
Ear length	127	152	152	152	152	178	190	203	203
Chest girth			686	737	813	864		965	1072
Weight in pounds	39	46	52	57	72	84	110	128	

moose udder is not large and is located high between the thighs. The calf starts supplementing its milk diet with browse at about one month of age. My field notes for August 23 describe one of the rare occasions that we have observed suckling: "A buckskin colored cow walked by us into the lake and grazed submerged vegetation for more than an hour. She then called softly. A calf on the opposite shore replied, and ran to meet the cow as she emerged from the water. The calf nursed for three and one-half minutes, butting vigorously at the udder all the while. Then the female and calf disappeared into the woods."

Weaning seems to occur early in September, although the calf remains close to its mother for some months more. By October the calf is more than half as tall as its mother and its coat has taken on an adult shade.

Relative development of the antlers is almost the only way of estimating the age of moose older than yearlings. The yearling has knobbed spikes not much longer than the ears. The next year the antlers are about twice the length of the ear and show a bilobed condition distally. From the third year on, a palm appears and grows, probably reaching a maximum between seven and ten years. Evidence of tooth wear seems to indicate that very old bulls have lighter antlers, possibly with more points. Also correlated with age is the time of shedding of velvet. The author has observed old bulls with whitened antlers in early September, at which time the smaller-antlered bulls are still in velvet. There is a corresponding difference in the time of dropping the antlers, the older bulls losing theirs first.

II. BEHAVIOR

Unlike the red deer studied by Darling (1937) and the elk or wapiti as studied by O. Murie (1951), the moose is almost unique among deer in being a solitary form without definite herd organization. This trait has several possible causes and several probable results of interest to the student of animal behavior. It means that the bull moose, unlike the bull elk, collects no "harem;" that the cow moose is solely responsible for the care of the calf without being able to turn it over to a nursery herd, and that the problems of "peck-order," leadership and social hierarchy would appear in their most elementary and primitive state in moose. In an attempt to gain some understanding of the ways by which a moose meets the exigencies of its environment alone and successfully, the author has spent approximately eighteen hundred hours in the actual observation of moose behavior.

CYCLIC PHENOMENA

Diurnal Cycles

During the summer months moose become active at about 4:00 or 4:30 A. M., or about an hour before dawn, moving from aspen or conifer thickets where they have spent the night into more open areas and ponds. They feed actively until the middle of the morning, or for about five hours. At about 9:30 A. M. they retire to beds or forms usually close to ponds and often in willow thickets. Here they may continue to browse occasionally while lying down, moving only if disturbed. Calf moose often doze at this time. In mid-afternoon the moose re-enter ponds or begin to browse once more. At full dark they may leave the places where they have been feeding and move into thickets, sometimes at a distance of more than a mile. A cow with a calf less than six weeks of age does not move as far at night and may simply use the midday rest area again. As day length decreases, the inception of activity is delayed and the midday "siesta" is shortened. This daily movement of moose is quite similar to that for elk but somewhat more restricted.

Annual Cycle

Moose spend their winters where food in the form of willow or aspen browse or hay is available and where the snow is not too deep. Wind-swept stretches on the river bottoms fill these requirements, as do certain south-facing slopes. The available niches are far fewer in winter so that at this time moose are found in their greatest aggregations on the relatively few favorable feeding areas. On a census flight in March, 1948, in Jackson Hole, we counted 65 moose. They were grouped along the Snake river bottoms as follows: two, four, six and five per group in one feeding area; two singles and a group of four on one aspen slope; two groups of two, two groups of three and one group of five in another area; two, five, three and one around a series of beaver ponds. This gives an average group size of two and eight-tenths individuals for the 23 groups. Five areas were observed with an average of four and eight-tenths groups per area. Where there is one rather isolated favorable area, 20 to 30 moose may often be found in it in the winter. As mentioned before, it is at this time that the moose come into closest contact with human beings.

Brown & Simon (1947) point out that, as is the case with other deer, winter is the critical period for moose. They say that those acquainted with the haystack manners of moose favor this species over the elk, because it feeds more cleanly, without scattering the hay over

the ground or trampling and mixing it with filth. Many moose, unlike elk, do not come in to take man-provided food every day, even though it is readily available. Of 37 moose wintering near Black Rock ranger station, only 22 were known to come in for hay, and those not constantly. These authors comment further on the status of orphan calves in winter. These were observed lying alone and in the same position for many days, until it seemed that they would never rise to browse willow again. However, close examination of their bed grounds often gave evidence that the young had been actively feeding, to such an extent that dense willow thickets were reduced to mere stumps.

This observation suggests caution in the interpretation of the significance of local areas of apparent over-browse. Brown & Simon mention that in the spring moose move onto sage flats and browse sage to a considerable extent. This plant has been observed by us to be a part of moose diet at other times of the year as well.

Still later in the spring the bulls and some barren cows follow the receding snow line to higher and higher elevations in a sort of altitudinal migration. Cows with calf apparently do not go so far or so high, but move back into very secluded areas for calving which takes place usually in May. Yearling calves usually remain near the cow throughout their second summer. Such cows with first-year calves move very little unless disturbed and may be observed in the same area of a few acres throughout the summer. These summer grounds are not held to the exclusion of other moose, which may drift in and out, forming loose temporary groupings of up to ten animals. During the summer months at least some bulls and dry cows wander as much as 30 or 40 miles, often moving across passes from one drainage to another. In late August and early September the older bulls attach themselves to cow-calf groups. At this time a typical group consists of the mature bull and cow and either a first year calf or a yearling calf, or sometimes both. My field notes describe the typical behavior of such a group (September 16, when the hunting season had been open about ten days): "At the mouth of Spread Creek where it enters the Snake, I noted a cow which stood perfectly still and looked in my direction for three or four minutes. A four-year-old bull, quite black, with white antlers moved out from behind willow bush between me and the cow. As the cow turned and entered the Snake, a this year's calf and a yearling got up from where she had been standing and followed her across the river. The bull followed the cow and calves." I watched this group for three more hours and saw it again the next day. There was no sign

of sexual behavior during this time. The bull stays with the cow (and calf or calves) for ten days to two weeks. Apparently he does not attempt to drive the calves away.

(September 17, Pelican Creek): "12:30 P.M.—Three-year-old male, female and this year's calf. The bull followed the cow quite closely as she moved, sniffing at her hindquarters but making no actual contact. At 5:45 P.M. still in the same area, the bull swings his head from side to side, beating his antlers against the brush, and runs around and around in a circle." (Next day, same place): "10:30 A.M.—The same group as yesterday moves slowly into sight, browsing on willow. Then the male moves out onto a sedge flat followed by the calf, which touches noses with him and stays very close to him as he crosses the stream. The cow crosses about fifteen minutes later and runs in a tight circle. The male now spends about one half hour rubbing his antlers on a spruce. Erection of the penis was intermittently apparent at this time."

Darling (1937) has noted the association of antler rubbing with erection and has referred to the situation as "masturbatory." It seems to this observer that the antler rubbing may be one stimulus-producing response in the sex drive-response complex, while erection represents a later similar response. In other words, these may be two results of the same complex of causes, and not have a simple cause and effect relationship between themselves, (Denniston, 1954).

Actual breeding apparently follows several days or even weeks of association of the bull with the cow. (September 23—Pelican Creek): "6:00 A.M.—One big bull with white-polished antler tips chases two younger bulls away from his wallow. He then squats, urinates in it, and paws the ground. He chases away a younger bull which comes up to paw at the edge of the wallow, then lies down and rolls in the wallow. He approaches a female standing within five yards of the wallow, and sniffs her hindquarters. Next the bull throws his head back, opens his mouth, and retracts his upper lip, holding this posture for three minutes. (This posture is exactly like that of a bull elk when bugling, but no sound was discernable to the observer at a distance of about sixty yards.) The bull now approaches the front of the female and shoulders her toward the wallow. At 7:30 A.M. he mounts her and thrusts four or five times. The female runs out from under him and runs in a circle, returning to the wallow. The bull mounts again and stays mounted for three minutes. They move out of sight of the observer behind dense willow, but the male's head and shoulders appear above them as he apparently mounts the cow a third time."

Wallow production is probably closer to the consummatory response in the time series of stimulus-producing responses in this sexual situation, and therefore possibly more of an essential component in the drive-arousing response series. Moose have been observed to breed in shallow ponds, but whenever circumstances permitted, a wallow was observed on the bank.

INDIVIDUAL BEHAVIOR

Development of Behavior

Since it was rather rare to see two calves together, most of the apparent play observed was solitary gamboling and exploration. The author is well aware of the potential pitfalls in characterizing a given activity as play, which have been pointed out by Beach (1945). Nevertheless, the term perhaps serves as a useful descriptive label for certain aspects of juvenile behavior which have no apparent immediate utility.

The orphan calf moose observed regularly during the summer of 1948 afforded a unique opportunity for the study of the play patterns of *Alces*. For the first month of her life no play-like activity was apparent. At about one month of age she would push back when pushed gently on the forehead and would push gently at the observer on her own initiative. When two months old she would "play" with a lawn sprinkler, striking at it with her forefeet, biting it and running back and forth through the spray. A little later she would run around and around any fair-sized structure such as a shed or barn. This running in circles was also shown by mature females in situations of a sexual nature. At about the same age she would strike at the whiffletree of a carriage with her head or forefeet, dodging back quickly to avoid the rebound of the other end. A little later she had to be confined to a corral, as she would repeatedly run and butt at some of the smaller children on the ranch where she was fed. At no time during such activities, or even when being restrained for her weekly weighing and measuring, did she show any component of the adult "rage" pattern.

Several times in late August three-months-old calves were observed to beat with their heads at low brush, a pattern otherwise shown by males in rut.

Play-like activities by more adult moose were noted. A young barren cow feeding in the same large pond as a mature bull reared several times and splashed down, then cantered through the water past the bull, sending great sheets of water over him. Then she turned around and bleated softly. The bull moved slowly out of the pond, in the opposite direction. A sixteen-months-old bull with antlers still in velvet was observed to run several times towards a small willow clump

and veer off just as he reached it. After several such runs he put one antler under a small bunch of twigs and tossed it, repeating this action several times.

Other differences between juvenile and adult behavior were somewhat similar to those seen in many species. A two-months-old calf was much more restless than the cow, moving about constantly while the latter stayed in one place or moved along slowly, browsing as she went. The calf showed apparent curiosity or interest by interruption of other activities and orientation of the receptors to many natural sounds to which its mother gave no outward sign of attention. The calf was much more vocal than its mother, often emitting a two-note blatt repeatedly. The calf fed much more intermittently than did its mother and sampled many things not included in the adult diet. (See section on Foods and Feeding.)

Behavior Associated with Aggression

Just as it is impossible to state definitely that certain behavior represents play, so, technically, one cannot label another type of behavior as "anger." There are nevertheless changes in moose behavior associated with certain situations that impress the observer with the necessity for cautious procedure on his part. In other words, although the laboratory psychologist might object to the field observer's characterization of a moose's behavior as anger, the latter is often in no doubt that he had better climb a tree when he sees such behavior. This "rage" pattern of moose was most frequently observed in cows with young calves at the side. It was not shown by bulls in rut except when driving other bulls from a wallow. It was seen in many moose cornered by snow in winter. In this pattern the mane is erected, the ears flattened back against the neck, the lips retracted, the tongue protruded and curled up over the upper lip and nose and repeatedly darted in and out, licking the upper lip. The animal usually rears on its hind legs, pawing the air with the forefeet, if the stimulus object is at a distance of less than about forty feet. In a more distant encounter the animal usually lowers the head while showing the rest of the pattern. That this pattern may represent a bluff or threat is apparent from several encounters the author has had with moose. A representative experience is quoted from a note made in the field: "July 22, Canyon southwest of Brooks Lake. Surprised a cow moose and small calf at less than forty feet as I topped a rise on the trail. The horse shied and trembled as the cow whirled toward me, pivoting on her hind feet. Her mane was erected and her ears flattened back. She licked her nose very rapidly.

I wheeled the horse, tied him out of sight, and returned on foot. The moose were feeding quietly on willow at the bottom of the canyon about 100 feet below me. They showed no sign of emotional disturbance." That this behavior pattern serves the function of warning animals encountered by moose so that actual conflict seldom ensues, and that moose will not charge until ample warning of this sort has been given, is borne out by a statement made by D. E. Hess, Supervisory Park Ranger of Yellowstone National Park (1951). Speaking of moose gathered about a salt block in the autumn, he says he was able to approach within eight to ten feet before the warning signs mentioned above were followed by a slow advance. He says further that every moose he encountered face to face or at a distance, in timber or open country, yielded the trail or gave a choice of going around it. The moose would not turn tail, but neither would it advance.

"Attention" Attitude

Another recognizable attitude or posture was one that impressed the observer as indicating something like attention or interest. By these terms we wish to imply no hypothetical autonomous central process of Hebb (1949), but rather a notable orientation of the receptors toward the source of an unusual change in the environment. In this condition the head is raised, the ears erected and turned forward, the nostrils dilated; "testing" type motions of the head were also in evidence. Further remarks on this posture will be found below under "Moose-Man Reactions."

SOCIAL BEHAVIOR

Intra-specific Relations

A. Mother-Young Relations

Because of the solitary nature of the moose, the juvenile individual is particularly dependent on its mother not only for sustenance but also for a sort of psychological guidance and protection. The young suckle for about two months, weaning being a gradual process. During the latter part of this time the calf samples many types of vegetation, including several not utilized by the adult, to an ever increasing extent. The young are reported to remain with their mother through their second year. Although close associations of mature females and second year calves were often observed, there was no way of proving the familial relationship. The female exerted a guardianship over her calf which varied from individual to individual and from time to time. The protection ranged from threats, if the observer approached too closely or surprised the animals, to apparent temporary

desertion. The calf played and explored fairly close to its mother and often lay down and rested in partial concealment near her while she browsed.

July 13, three miles south of Togwotee Pass: ". . . the female apparently alone. She watched us three to four minutes, then went over to willow screen and a young calf got up and followed the cow. After traveling about three yards this way the female waited and calf went ahead slowly." Less solicitude was shown by a cow at the ponds: ". . . the female walked off into the brush leaving the calf at the edge of the pond. The calf bleated quite loud and repeatedly (Myah—Myah—Myah) but the cow continued to move away. The calf, now bleating constantly, attempted to cross the mouth of a small feeder stream, became mired twice, finally struggled out and ran after the cow who was at the edge of a pine grove about 200 yards away and still moving."

The cows seemed completely indifferent to the near approach of bulls and other cows and were only mildly affected by calves other than their own.

The only evidence of communication involving vocalization in the maternal-young relationship, in addition to the instance already mentioned, was the following: "I was watching a mother and calf in a pond when suddenly there was repeated plaintive bleating and crashing of the brush and a grayish dogie calf approached the female. She blatted very softly, and the calf ran to her and licked her nose, and then ran on still calling."

A so-far unexplained dependence of the weaned young on the mother has been reported to me several times by competent observers. Daniels (1953) has commented on this situation. According to these reports, if the calf loses its mother as late as November, when it is seven or eight months old, it often does not survive, succumbing to exposure or malnutrition. There are at least two possible explanations for this situation. One is that the cow initiates movement from one locale to another. In the crucial winter period an inexperienced calf is likely to stay in an area of deep snow and poor browse until too weak to escape from it. (See Brown & Simon *op. cit.*). Secondly, if the calf is fortunate enough to find a good browse area, there will be other moose, elk and possibly deer using it. In these areas competition for browse is quite keen, both intra-specifically and inter-specifically. Without the protection afforded by the cow, a calf is truly at the bottom of the "peck-order," and suffers the fate of similar unfortunate individuals of other species.

B. Male-Young Relations

The mature bull moose appears to be very tolerant of first year calves even during rut. We have never observed a bull attempt to drive a young calf away from the cow's side, even during the height of sexual activity. The calf seems to reciprocate and often follows and associates with a bull that has joined the family group early in the breeding season. This could be an effect of "imprinting," with transfer from the mother to any large-size moose. The bull seems to become somewhat less tolerant on the winter feed grounds, however.

C. Male-Male Relations

As mentioned in other sections of this report, during much of the year bulls may associate in loose groups of as many as half a dozen individuals, although the most common grouping is a pair of bulls. Very little social interaction is observable in such groups throughout the year, with two exceptions. A mature bull will defend his "breeding wallow" against other males. This is the only form of territory defense noted in almost two thousand hours of observation. Males will "threaten" other males on a winter feed ground, but this is true of all mature moose in such a situation. There is some indication that the largest and most mature bull takes the initiative in group action. He often seems to occupy the first position when a group of males moves from forest out to feed on willow flats or in other similar movements. This may represent a generalization from the juvenile situation on the part of the smaller bulls. They are early dependent on a larger moose (the mother) and learn the habit of following it. The cue of larger size may then become associated with following such an individual and be transferred to the largest bull in an all-male group.

This observer has noted "mock combat" between two- and three-year-old bulls on several occasions. They run toward each other and then "wrestle" by means of their antlers, even when these are still in velvet. James Simon, at the time he was Director of the Jackson Hole Research Station, reported a pair of young bulls "very carefully rubbing each other's antlers." In view of the possible erogenous nature of deer antlers, as indicated by Darling (*op. cit.*), such observations are suggestive of possible homosexual activity.

On two occasions we observed the largest bull in the group walk in between such a pair of antagonists, and once a mature bull walked between the observer and a two-year-old bull which had adopted a "threatening" posture in relation to the observer.

The fact that more mature bulls come into

rut, i.e., under maximum sex hormone influence, before the younger males, may well contribute to this age dominance pattern, as well as insuring that most of the breeding will be done by bulls that have been successful in reaching maturity—an obviously adaptive situation from the point of heredity.

Actually, the observer is struck by the lack of social interaction between moose during most of the year. Moose of either sex may approach individuals or groups, feed as close as ten feet from them for hours, and then leave without a single individual changing its behavior in any way apparent to the observer. A rare exception to this lack of social response is recorded in our field notes: "August 6, 7:00 A.M. Two males were feeding on the near side of the ponds. One appeared disturbed by me as I attempted a closer approach, and ran across the pond splashing water in great sheets higher than his head. The second moose could not have discerned me but followed the first much more slowly."

Inter-specific Reactions

Because the moose is almost exclusively a browsing animal it is in minimum competition with other large mammals and with domestic stock, which are grazers. Also, since it is solitary, it does not have to compete with other members of a herd. As a possible result of this lack of competition, the moose seems not to have built up effective social habits that would enable it to obtain its share of food in a competitive situation. When a moose encounters other species on a winter feed ground it is at a definite disadvantage.

A. Moose-Elk

In the Rocky Mountain region the species most frequently co-inhabiting the moose's territory is the elk, a form with highly developed herd organization. When individuals of these two species come into conflict the elk is almost always successful. Daniels (*op. cit.*) has this to say: "I have seen a huge bull moose completely bullied by a cow elk, and sometimes even an elk calf will run a moose from a pile of hay. While the two species will mingle and feed together, the elk are antagonistic toward the moose and abuse them constantly."

B. Moose-Stock

Where moose and horses or cattle come into contact there seems to be very little open conflict. Many of the meadows where horses graze are bordered by willow on which moose browse. It is not uncommon to find moose mixed in with a herd of horses after a night's grazing and it is sometimes difficult to cut the moose out of

the herd when the horses are rounded up and brought into a corral.

If a large group of cattle is moved onto summer range, moose seem to move out of the bordering willows and never associate as closely with the cattle as they do with horses. However, under the hardships of winter moose will come into corrals where hay has been put out for cattle. At such times they are perforce in fairly close contact with cattle, but nevertheless little overt friction is observed.

C. Moose-Predator

In the territory of the Shiras moose, almost the only effective predator is man. Coyotes and bob-cats would represent some danger to calves if it were not for the effective protection afforded them by their mothers well into their second year. Mountain lions and bears, both black and grizzly, possibly could prey on two- or three-year-old moose. There are at least two recent confirmed reports of such predation by bears in the Glacier National Park area. One of these was by a grizzly and one by a very large black bear.

Possibly because of the lack of predation, moose have the habit of standing and orienting their receptors toward the source of any disturbance. This pattern is in contrast with that of elk and deer under similar circumstances. These animals go bounding off immediately. The moose's delay in taking flight makes it extremely vulnerable to hunters.

D. Moose-Man

Like many animals, moose tolerate a quiet, unobtrusive observer who makes no loud noises or quick motions. If he remains downwind and motionless, moose may approach very close or they may be observed for hours without being disturbed. August 12, 5:00 P.M.: "... while sitting on a log in an alder thicket, three paces from a moose trail, I observed a very large female walk slowly up the trail toward me, approaching with the wind. Just previously I had heard the loud voices of a surveying crew. When the female was barely past me, she stopped and looked hard at me for about thirty seconds then went on silently. Her tracks looked as though she had been walking on tip-toe."

The next day I watched and photographed a two-year-old bull from 9:30-11:00 A.M. When some tourists stopped their car nearby and approached the ponds, talking in fairly loud tones, the moose dashed into the cover of the brush.

Moose will often circle a quiet observer, moving very silently and swiftly even in rather dry brush. July 10: "I crept through brush till I came opposite the bull without being seen. He

browsed willow at end of growth on island, then crossed seventy yards downstream to my side; this from 7:45-8:10 A.M. I heard a few twigs snap and then saw movement about thirty yards behind and above me. The moose then recrossed to the island at 8:45, having made a complete circle around me."

The "attention" of moose (meaning pre-existing set in the Hebbian sense) often does not seem to depend on the quantity of environmental change. Thus, when the observer's efforts at quiet stalking fail, they seem to disturb the moose more than much stronger, but less stealthy, stimuli. A somewhat amusing incident from my field notes illustrates this point. September 7, Pelican Creek: "A two-year-old bull with a bloody antler tip partly in velvet was browsing on a willow flat. Later he was joined by a female and a large white-antlered bull. Still later tourists yelled and whistled at them without much apparent effect. I walked about a half mile down to the end of the ridge. I tried to walk very quietly and to keep out of sight in returning. The old white-antlered bull was somewhat nearer the ridge and a little separated from the others. He looked toward me with ears turned forward, then shook his head and trotted away." Evidently on this occasion my efforts at stalking disturbed this moose more than all the noise made by the tourists.

Moose can be provoked into aggression or threats even during the summer but, as Hess (1951) aptly remarks, "anyone attacked by a moose must really have asked for it."

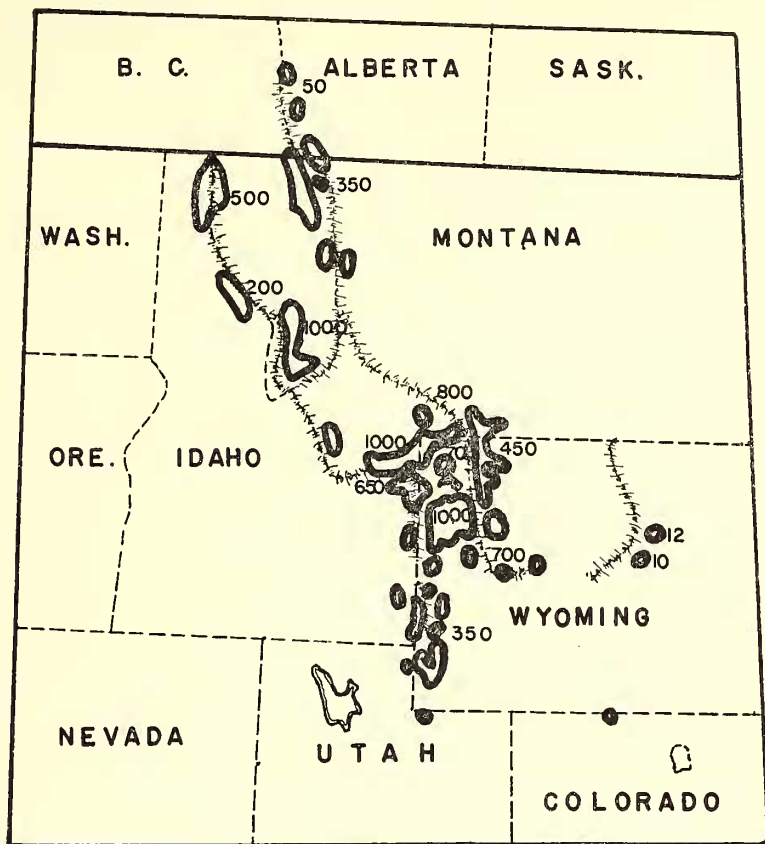
Dr. Robert Rausch, a co-worker at the Jackson Hole Research Station, did "ask for it" on one occasion. In early June he encountered a cow with young twin calves and in order to test their reactions he yelled and threw sticks until the female trotted toward him in a "rage" attitude. He climbed a small tree, carrying his collecting shotgun. While treed he noticed a raven that he wished for a specimen, so he shot it down. The cow moose ran to the raven and completely macerated it with the hooves of her forefeet.

It is much less difficult to get moose to attack in the winter and most moose-human encounters occur at this time. Daniels (1953) tells of being charged repeatedly by a moose in a large hay barn in winter. Brown & Simon (1947) reported being chased through the snow and brush by a young moose they were trying to feed. Attacks on automobiles by moose trapped on the highways by high banks of snow have been mentioned previously.

III. POPULATION DYNAMICS

Present Distribution

The area studied most intensively in this paper

TEXT-FIG. 1. Present distribution of *Alces alces shirasi*.

is the type location for *Alces alces shirasi* and also one of the areas of the greatest abundance of the subspecies. (See Text-figure 1). At the present time there are between 3,000 and 4,000 moose in and around Yellowstone National Park. The protection afforded by the Park to an unmolested breeding nucleus has played some role in this concentration, but the naturally favorable habitat is probably of almost equal importance. An interesting aspect of this abundance is its rather recent occurrence. The moose population of the Park itself is holding steady at about 700 animals and there are now between 1,000 and 1,100 moose in Jackson Hole just south of Yellowstone Park. From Jackson Hole proper the animals seem to be spreading south across the Gros Ventre River to the upper Green River, where they have increased to 700, and southeast onto the upper Wind River, where there are only a few less. The latter region is one of the few where Shiras moose may be overcrowding their range. The Forest Service and the Wyoming Game and Fish Department have established special exclusion plots north of DuBois to study this situation. A few moose have appeared as

far south as Lander on both sides of the Wind River Range.

To the west lies a second area which comprises several rather isolated groups of moose on both sides of the Salt River Range. There may be as many as 350 animals here. These appear to have come rather recently almost straight south from the Hoback, although Robert Patterson of the Wyoming Game and Fish Department tells me of seeing a few moose well out in the Red Desert, so that some animals could have come across from the south end of the Wind River Range.

In the Sunlight Basin area, east of Yellowstone Park, the moose population of some 150 is reported to be barely maintaining itself. This is in spite of apparently abundant browse. Recent heavy snows and severe winters in this basin may be limiting the population.

There are approximately 35 moose on the Owl Creek hills in the northern section of the Wind River Shoshone-Arapahoe Indian Reservation. The southern limit of distribution of a constant population is probably Kemmerer.

Durrant (1952) states that the moose is

sporadic in Utah and that they are known to occur in the Uinta Mountains and in the Wasatch Mountains as far south as Utah County. Accidental individuals have been reported in Logan Canyon and near Lewiston. In 1947 a bull was killed in Ogden Canyon. In summary, moose occasionally are seen near the State line around the southwest corner of Wyoming.

The even rarer accidental moose in Colorado may come from this small Utah population or from nearby southwestern Wyoming. In 1941 a moose was shot near Steamboat Springs, Colorado. It is reported that Milton Estes shot a moose in what is now the Rocky Mountain National Park in the 1860s.

Dalquest (1948) refers to the casual occurrence of moose in Washington. He assumes that they came south from Canada, so that they may have been *A. a. andersoni* and not the Shiras subspecies. (See also Peterson (1950)).

In Idaho there is a little group of moose south of Gray's Lake and another group in Targhee National Forest southwest of Yellowstone National Park. A big game census made in 1950 by W. M. Shaw, Idaho State Conservation Officer, recorded 642 moose in Targhee forest of Idaho. Moose here and in the Beaverhead Forest northwest of the Park, where there are about 1,000 animals, have shown a gradual increase in recent years. North of the Park in the Gallatin Forest there are now approximately 790 head. This area was almost devoid of moose in 1910, so that they have shown a remarkable comeback, probably aided by migration from the protected breeding stock in the Park. These areas adjacent to the Park contain about half the moose in Montana, whose estimated total population is 3,587 animals. These southern areas are the only ones in Montana open to hunting of moose. Some 1,200 animals are reported for the Bitterroot Forest south of Missoula, although we feel that this may be somewhat of an over-estimate. Two groups of animals totaling 700 extend north and west along the Bitterroot range toward Coeur d'Alene. These groups and the 350 animals in and adjacent to Glacier Park do not seem to be reproducing adequately and are diminishing in numbers despite a lack of hunting pressure. In Glacier Park itself there are estimated to be 155 moose, with about 40 animals in Canada's adjacent Watertown Lakes Park. This population is barely maintaining itself.

In 1948 and 1950 the Wyoming Game and Fish Department transplanted two groups of about eight moose each to the east slope of the Big Horns about 100 miles east of the previous extremity of their range. These moose are said to be establishing themselves satisfactorily, and reproducing.

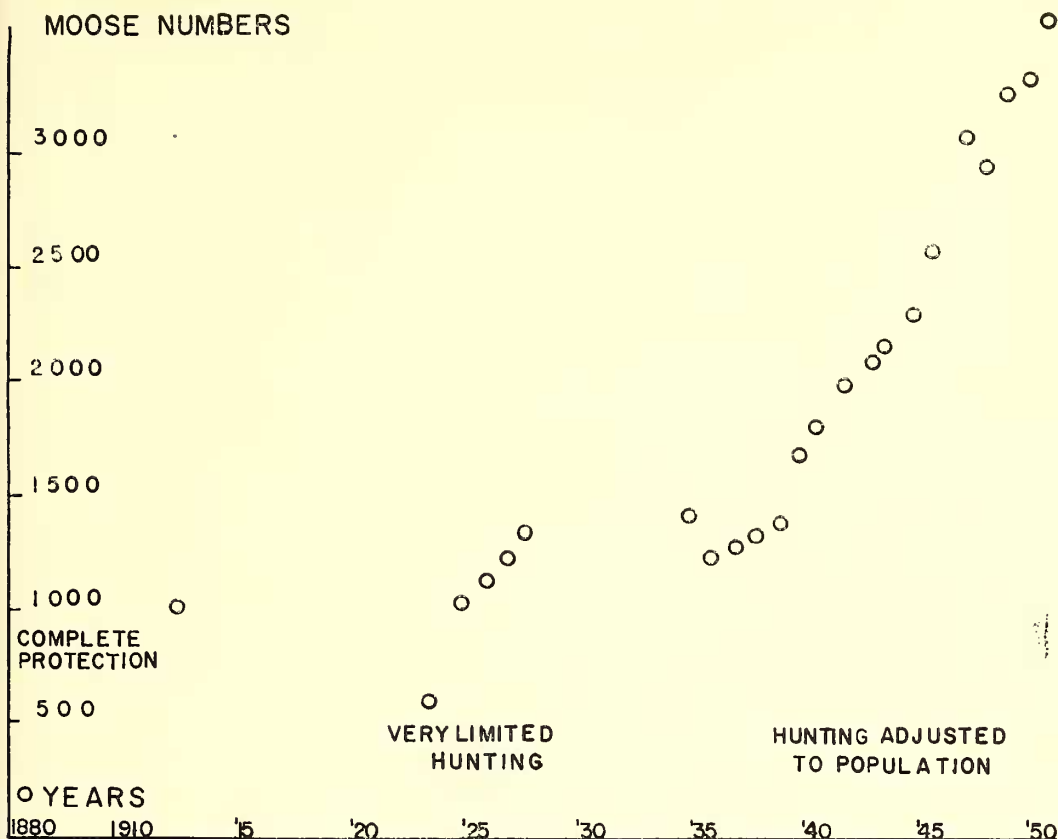
To summarize, it is estimated that there are today about 3,763 moose in Wyoming, including the Yellowstone National Park; 3,587 in Montana, and almost 1,000 in Idaho, Utah, Colorado and the Watertown Lakes area of Canada—in all, somewhat more than 8,000 individuals of *Alces alces shirasi*.

Relation between Counts and Estimated Totals

The proportion of the total population seen during a census check obviously depends on the methods employed. Even an experienced observer traveling casually will obtain only a very rough idea of the numbers of moose in the country through which he passes. More accurate is an airplane census in mid-winter. Similarly, an experienced observer living in a given small area for some length of time and systematically recording his observations may make a close estimate of the numbers of moose in the area. In this respect it is interesting to note the downward trend of estimates when the latter are based on objective data. In a series of reports to the Secretary of the Interior from the Superintendents of Yellowstone National Park we find the following: 1919 . . . "slightly more than 500 moose." 1920 . . . "I believe that there are about 800 moose in the Park." In 1924 and subsequent years the estimate of population was based on actual counts: 1924: count—121, estimate—385; 1925: count—170, estimate—525; 1926: count—103, estimate—575; 1927: count—73, estimate—600; 1928: count—111, estimate—650. Apparently when the population in the Park reached about its present level of 700 moose, the area had reached a saturation point and moose started to move out of the Park in increasing numbers, so that Wyoming was able to allow hunting. In 1912 the State Game Warden estimated the state population at 500 head and 50 hunting permits were issued. The number of permits remained constant for the next few years. We believe that the average legal kill in Wyoming represents about 8 per cent. of the total state population each year in terms of a sliding average. (See Text-figure 2).

The factors behind certain aspects of moose distribution seem fairly evident, while others are still puzzling. *Alces alces shirasi* must have established itself when it lost its connection with the much larger population of *A. a. andersoni* in Canada. This connection was later reestablished, giving a small area of overlap in Canada.

Shortly before the turn of the century the numbers of *A. a. shirasi* reached a dangerously low point. Thus Henry Avare, Montana State Game Warden, declared in 1910, "When the Game Warden's department was created ten years ago, these animals were practically ex-



TEXT-FIG. 2. Moose population changes in Wyoming and Yellowstone Park.

tinct in the state. Today, after ten years of careful protection, there are probably 300 moose in Montana. . .” In the forty-five years since 1910 there has been a ten-fold increase in moose in Montana, corresponding to the general trend in moose population elsewhere in recent years. As a practically monogynous deer, moose are peculiarly susceptible to hunting pressure, even if hunting is limited to bulls, since a bull usually mates with only one cow per season. Conversely, they have responded markedly to easing of hunting pressure through game law enforcement and the complete protection afforded by Yellowstone Park to a breeding nucleus. This response has taken the form of a great increase in numbers and a spreading to the south and east so that moose have been seen during the last dozen years where they have never been seen before.

SUMMARY

I

The behavior and ecology of the moose as made manifest in this study of the Wyoming or Rocky Mountain subspecies, *Alces alces shirasi*,

are unique among deer to the extent that the moose is a solitary, somewhat amphibious form.

The daily cycle shows early and late feeding periods on littoral or aquatic flora. During the warmer part of the year these feeding periods are interrupted by a mid-day rest.

The annual cycle finds the moose in its greatest aggregations on winter food grounds, although Shiras moose do not form yards. Winter is the most difficult time for moose, bringing them into contact with man, stock and other game. Possibly because of the lack of effective social patterns occasioned by their solitary lives, moose are often inadequate in competition for food and space. Orphan calves may have a difficult time living through the winter, in the absence of the protection and leadership normally afforded by the mother. Most moose “attacks” on human beings come at this time of year. In the spring the winter aggregations split up with pregnant cows moving into secluded back country for calving. Bulls, and to a lesser extent dry cows, show a limited altitudinal migration in spring, following the snow line to graze on new

grass and browse on sage. From the time of their birth in May the calves are particularly dependent on their mothers. Since the moose has no nursery herd this dependence is accentuated, and "imprinting" in the Tinbergen sense may be to a single large individual, whereas in a herd form like the elk such "imprinting" may be to the herd itself. The reproductive behavior of the moose is unique among deer in that the male must attach himself to a cow-calf group and remains with a single cow for some weeks.

II

Alces alces shirasi apparently established itself as a subspecies when it lost its connection with the much larger population of *A. a. andersoni* to the north. After subspeciation had been completed the Shiras moose increased its range so that there is now a small area of overlap with the presumed parental stock in southern Alberta and British Columbia. At about the turn of the century the Shiras moose was nearly extinct, probably due to uncontrolled hunting. The protection afforded a breeding nucleus by the policies of Yellowstone National Park and the various State game and fish departments has enabled the subspecies to increase its numbers to more than 8,000 individuals, and its range to parts of six States and two Provinces.

BIBLIOGRAPHY

- ALDOUS, S. E. & L. W. KREFTING
1946. The present status of moose on Isle Royale. N. Amer. Wildlife Conf. 11 pp. 296-308.
- ASDELL, S. A.
1946. Patterns of Mammalian Reproduction. Comstock Publishing Co. Ithaca, N. Y.
- BEACH, F. A.
1945. Concepts of play in animals. Amer. Nat. LXXIX.
- BROWN, R. C. & J. R. SIMON
1947. Notes on wintering moose. Wyoming Wild Life. XI, pp. 4-8. June.
- DALQUEST, W. W.
1948. Mammals of Washington. Univ. of Kansas, Publ. Mus. of Nat. Hist. 2.
- DANIELS, T. W.
1953. Winter at Blackrock. Wyoming Wild Life. XVII, pp. 20-27. Feb.
- DARLING, F. FRASER
1937. A Herd of Red Deer. Oxford University Press, London.
- DENNISTON, R. H., II
1954. A comparison of the natural responses and a recently learned response as an expression of the sex drive level. (abstract) Bull. Ecol. Soc. of Amer., vol. 35.
- DURRANT, S. D.
1952. Mammals of Utah. Univ. of Kansas Publ. Mus. of Nat. Hist. 6.
- HEBB, D. O.
1949. The Organization of Behavior. John Wiley and Sons, N. Y.
- HESS, D. E.
1951. Moose molesting. Yellowstone Nature Notes. XXV, March-April.
- HOSLEY, N. W.
1949. The moose and its ecology. Wildlife Leaflet 312, U. S. Dept. of Int., Washington, D. C.
- MERRILL, S.
1916. The Moose Book. E. P. Dutton Co. New York, N. Y.
- MURIE, A.
1934. The moose of Isle Royale. U. of Mich. Museum of Zoology Misc. Pub. No. 25.
- MURIE, O.
1951. The Elk of North America. Stackpole, Harrisburg, Pa.
- PETERSON, R. L.
1950. A new subspecies of moose from North America. Occasional Papers of the Roy. Ont. Mus. No. 9.
- ROBERTS, L. W.
1953. Technique for the extraction of chlorophyll pigments. Turtox News, vol. 31, p. 211.
- SETON, E. T.
1928. Lives of the Game Animals. 3, p. 151.